

OBSERVATIONS ON THE BIOLOGY OF  
*PALLIDOTETTIX NULLARBORENSIS* RICHARDS  
(RHAPHIDOPHORIDAE : ORTHOPTERA) FROM THE  
NULLARBOR PLAIN.

AOLA M. RICHARDS

*School of Zoology, University of New South Wales, Sydney*

(One text figure)

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*Synopsis*

The complete life cycle of *Pallidotettix nullarborensis* Richards probably takes up to two and a half years: about 11 to 12 months being required for the development of the egg; 11 to 12 months for the nymphal instars; and possibly five to six months for the adult. Females mature in late summer and males in autumn. Oviposition occurs during the winter months. First instar nymphs appear in late autumn, so embryos probably undergo a summer diapause. Seven pre-adult instars are passed through. Usually only one generation is present in the population. *P. nullarborensis* is the first species of Macropathinae to exhibit signs of cave adaptation. Although scavengers, *P. nullarborensis* are primarily carnivorous and arthropods are their main food source. They will feed on both live and dead tissues. Their predation on newly hatched chicks is only the second record of such behaviour by Rhaphidophoridae. Activity rhythms are similar to those of other Australasian Macropathinae.

INTRODUCTION

The Nullarbor Plain is a low plateau of Tertiary limestone about 75,000 square miles in extent, situated in south-western Australia. Only one species of Rhaphidophoridae, *Pallidotettix nullarborensis* Richards (Richards, 1968b), is known from the Nullarbor Plain. It has been collected from 24 caves, and observed in three others. Its distribution ranges from White Wells Cave (N14)\* in the far east, to Gecko Cave (N51) at the western extremity of the limestone, a distance of about 450 miles, and as far north from the coast as Lynch Cave (N60) near Loongana on the Transcontinental Railway. So far no specimens have been collected from caves on the Roe Plain to the south. *P. nullarborensis* appears to be confined to the limits of the Nullarbor Limestone.

The country immediately to the west of the Plain consists of low hills on crystalline Precambrian rocks with shallow overhangs, but lacking tunnels, while vegetation is semi-arid mallee. Although there are large areas of limestone southwest of the Plain, this combination of vegetation and geology appears to form an effective barrier against westward migration of Rhaphidophoridae. To the east of the Plain dune limestone occurs, stretching east to Lake Hamilton. Although it is possible there are caves in this limestone, the nearest recorded caves are approximately 300 miles to the south-east, and no Rhaphidophoridae have been collected from them. To the north of the Plain is the barrier of the Great Victoria Desert, while to the south lies the Great Australian Bight. The closest known Rhaphidophoridae come from the Adelaide district.

\*The Nullarbor caves and dolines have been indexed by the Australian Speleological Federation, and the numbers are prefixed by the letter N. This system is used throughout this paper (Hill, 1967).

*P. nullarborensis* is very abundant in some caves and poorly represented in others. In Moonera Tank Cave (N53), Murra-el-elevyn Cave (N47) and Horseshoe Cave (N59) large populations have been recorded one season and small ones the next. This may be explained by possible migration of the insects from one cave system to another (Richards, in press). In most caves they occur in the twilight zone close to entrances, but they have also been observed in regions of total darkness. In shallow caves they may extend throughout the whole cave system, and in deep caves they may occur up to 0.5 miles from the entrance. They have been observed on bat guano mounds 150 feet and 650 to 700 feet inside Murra-el-elevyn Cave, and they have also been collected from the large, steep doline leading down to this cave. In Cocklebidy Cave (N48) they have been taken from the main chamber, and also from the island in the lake, 800 feet inside the cave (Lowry, 1964).

During 1965, 1966, and 1968, D. C. and J. W. Lowry collected representative samples of all instars of *P. nullarborensis* for the author from 13 of the Nullarbor caves, and made many valuable observations on its biology. In early 1968, the author visited 12 of the caves, and further observations were made on the life cycle and activity rhythms of the rhabdiphorids. As a result, it has been possible to determine the complete life cycle and number of pre-adult instars, food preferences and reactions to different epigeal climatic conditions. This information has been compared with previous findings by the author (Richards, 1961, 1962, 1965, 1968a) and overseas workers (Chopard, 1959; Remy, 1931) on the biology of the Rhabdiphoridae.

#### LIFE CYCLE

*P. nullarborensis* has not been reared under observation from egg to adult. However, comparison of a series of measurements of selected anatomical features in a sample of 100 specimens shows that it is possible to divide the insects into a series of distinct groups ranging from first instar nymphs to adult insects. Sizes of individuals within each instar vary slightly, so mean values have been used in all cases. These indicate that seven pre-adult instars are passed through by both male and female insects (Figure 1). The appendage undergoing the greatest increase in growth at each ecdysis is the ovipositor. Not appearing until the third instar, by the time the adult instar is reached the ovipositor is 0.8 the length of the body.

To check whether an instar had been overlooked, the logarithm of the linear measurements of the hind femora were plotted against instars. Calculated values were obtained from fitted regression lines and are given in Table 1. The approximation of observed to calculated measurements is sufficiently close to remove the possibility of an instar having been overlooked.

Nymphs form the largest portion of any rhabdiphorid population. Table 2 shows the seasonal distribution of instars among a representative sample of *P. nullarborensis* specimens collected from Nullarbor caves during 1965, 1966 and 1968. The monthly sample size is variable, and the numbers of specimens collected at certain times of the year are admittedly small. Most samples were taken during 1966. All months are represented except March and July. The table does not show the abundance of each instar in relation to the total population, but the more abundant instars form the major portion of the larger samples. No difference in instar size or abundance of specific instars were observed in samples collected from different caves at the same period.

In the December and January sample, the sex ratio of nymphs is approximately equal, 29 females: 34 males, and most nymphs are in fifth or sixth

instars. Few adults are present during these two months, and only females have been collected. Although searched for, no males have been observed. Only two penultimate instar males have been collected, both in January.

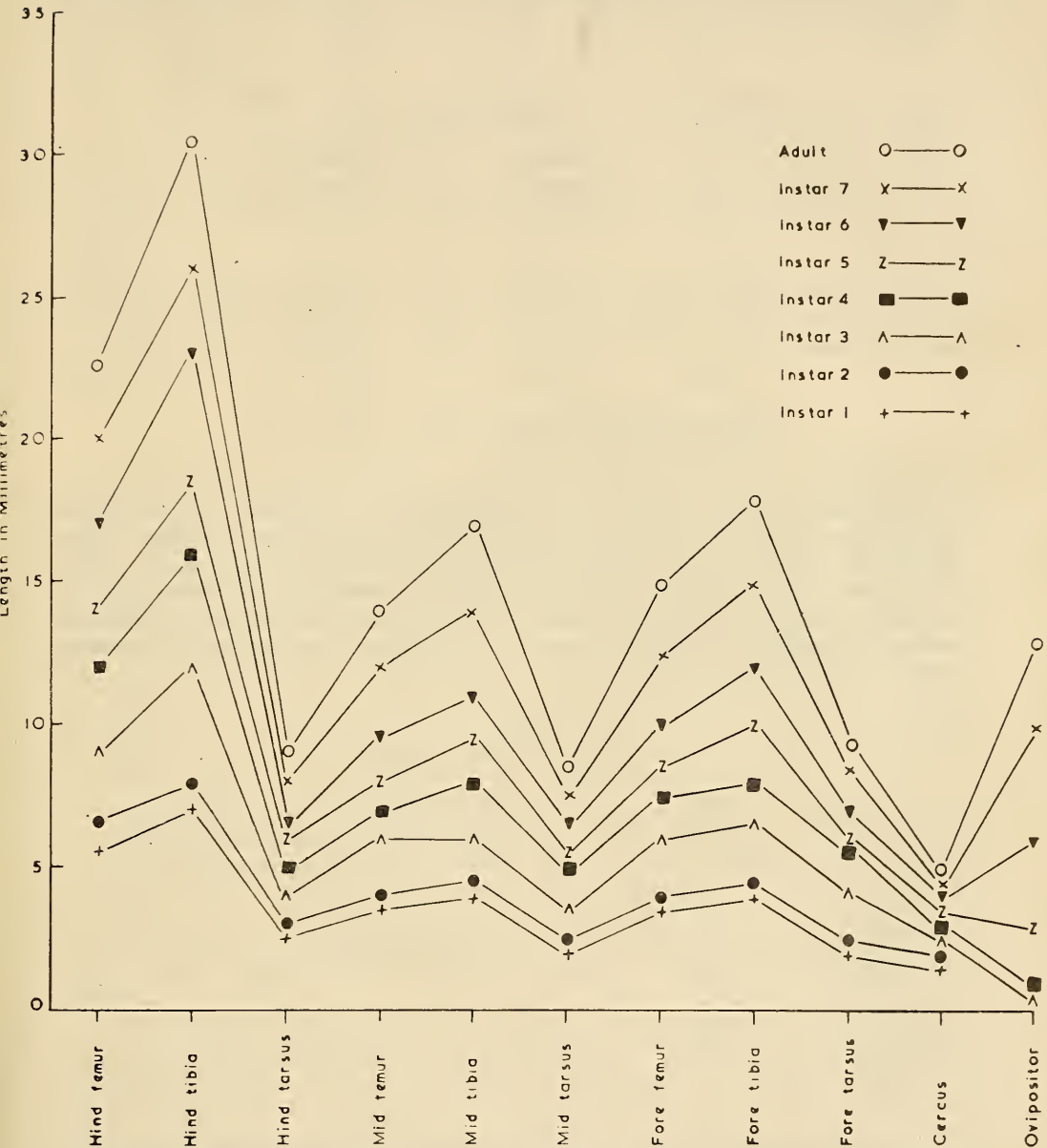


Fig. 1. Length of bodily structures in the several instars of *Pallidotettix nullarborensis* Richards.

In early February, the sex ratio of nymphs is again approximately equal. Most nymphs are in sixth instar, but a few females have moulted to seventh instar. In February 1968, only two adults, a male and a female, were observed out of a sample of 150 insects studied in three caves. They were in the preliminary mating attitude. There were no signs of oviposition.

In autumn, the proportion of adults in the population increases. Adult and seventh instar males and females have been taken in late April, May and June. During this period the number of nymphs decreases markedly, and the whole population is considerably smaller. First instar nymphs appear in May and June, and from then on they form the major part of the population.

TABLE 1  
*Fit of Dyar's Law to instar measurements of hind femora in P. nullarborensis*

Instar	Observed Length (mm.)	Calculated Length* (mm.)
1	5.5	5.8
2	6.5	7.1
3	9.0	8.7
4	12.0	10.8
5	14.0	13.3
6	17.0	16.3
7	20.0	20.1
Adult	22.5	24.8

Proportionality constant: 1.23.  
\* From regression line.

By September and October, the population has noticeably increased in numbers, and consists mainly of fourth and fifth instar nymphs. They gradually increase in size till they become adult the following autumn. Dead adults have been found in the caves in October. Odd specimens belonging to any instar may occur in the population, for example one adult female collected in early December, but they cannot be considered as part of the general pattern of the life cycle.

TABLE 2  
*Seasonal distribution of instars*

Month	Total Sample	Nymphal Instars							Adult
		1	2	3	4	5	6	7	
May .. ..	8	—	3	—	—	—	2	1	2
June .. ..	5	1	—	1	—	—	1	—	2
August .. .	2	—	—	1	—	1	—	—	—
September ..	4	—	—	—	2	1	—	—	1
October .. .	33	—	—	3	13	11	3	2	1
November ..	12	—	—	1	4	4	2	1	—
December ..	14	—	—	—	2	5	4	1	2
January .. .	64	—	—	1	7	26	23	2	5
February ..	150	—	—	—	—	40	99	9	2
April .. .	4	—	—	—	—	—	2	1	1

After the final ecdysis, a maturation period of several weeks must elapse while the gonads mature. The ovaries of 13 adult females have been examined. Two females taken in early December and early January had small ovaries and no mature eggs. Other females collected in late December, early January, May, September and October were gravid, with one large, fully developed egg. The egg is of a cream colour, oval in shape, 5 mm. in length and 2 mm. in width. It fills the greater part of the abdominal cavity. A female collected in May was the only exception to this rule, with five mature eggs inside

its abdomen. It is not suggested that only one egg is laid by each female, but that usually only one egg matures at a time. Maturation, mating and oviposition occur in the cooler part of the year, and mating and oviposition may continue for several months. As first instar nymphs do not appear till late autumn, embryonic development must take about 11 to 12 months, and because of high temperatures during the summer months, embryos may undergo a summer diapause.

The length of the nymphal period varies. In some nymphs an instar may extend over a longer period than in others, so it is common to find several different instars in the population at the same time. However, except during the winter months, usually only one generation of nymphs is present (Table 2). The duration of time spent in nymphal instars is about 11 to 12 months.

The adult life span is not known. However as adults are present in reasonable numbers in April, May and June, and dead adults have been found in October, this suggests a possible life span of five to six months. Thus the complete life cycle from oviposition to death is probably about two and a half years, or about 18 months from eclosion to death.

#### DEVELOPMENT OF CAVERNICOLOUS CHARACTERS

*Pallidotettix nullarborensis* shows a greater tendency towards cave adaptation than related species in southern and south-eastern Australia, but should still be classed as a troglophile. No degeneration of the eyes has been observed, but a loss of pigmentation has occurred in both nymphs and adults, so that it is the palest Australian raphidophorid species known (Richards, 1968b). There has also been a narrowing and elongation of the limbs.

All Australian Raphidophoridae examined by the author have very elongated appendages, and all but one occur in limestone caves. *Australotettix montanus* Richards, the largest known Australian species, is an epigeal form from the Blue Mountains of New South Wales. With a body length of 15 mm., the ratio of length of hind leg to length of body in the adult male *A. montanus* is 6:1. By comparison, the adult male *P. nullarborensis* with a similar body length has a ratio of 4.8 : 1.

A comparison of the range and mean of total leg length in eight species of Australian Raphidophoridae (Table 3) shows that *P. nullarborensis* has the fourth highest mean among males, and the third highest mean among females. However, using the ratio of total leg length to maximum width of the hind femur, and allowing for sexual dimorphism in most species, Table 3 also shows that *P. nullarborensis* has a much higher ratio than any of the other species. This is due to longer fore and middle legs, and a narrower hind femur.

A comparison of increase in leg length from instar to instar can be made between nymphs of *P. nullarborensis* (Figure 1) and those of *Micropathus cavernicola* Richards and *M. tasmaniensis* Richards, two raphidophorids of comparable size from Tasmania (Richards, 1968a). *M. cavernicola* has the largest tarsus mean length, while *P. nullarborensis* shows the largest femur means, but although these two features are fairly consistent over the fore leg, middle leg and hind leg, and the eight instars, their magnitudes are only of the order of 1 mm. even in the later instars. *P. nullarborensis* very consistently has the largest tibia means, and in the last three instars, the means of the hind leg are about 5 mm. greater than those for the other two species. The consistency, but not the magnitude of these three features are shown in Table 4, which gives for each segment the number of occasions (out of  $24 = 3 \times 8$ ) that the named species had the highest, or equal highest mean.

TABLE 3  
 Comparison of leg length and attenuation in eight species of Australian Rhaphidophoridae

Species	Number of Specimens		Total Leg Length (mm.)			Total Leg Length/Max. Width Hind Femur			S.D.		
	♂	♀	Range		Mean	Range		Mean			
			♂	♀		♂	♀				
<i>Pallidotetix nullarborensis</i>	12	14	142.0-150.0	132.5-141.0	146.0	136.1	45.5-52.2	44.2-47.0	49.8	45.4	1.5
<i>Australotetix montanus</i> ..	16	12	183.0-203.5	139.5-148.5	194.2	144.5	38.8-45.2	28.7-33.0	42.1	31.6	1.9
<i>Novotetix naracoortensis</i>	18	12	143.0-160.0	121.5-129.0	155.5	126.0	38.6-43.1	30.4-32.3	39.5	31.5	0.9
<i>Australotetix carraniensis</i>	14	16	161.5-179.0	131.0-144.0	172.1	137.1	35.9-39.7	29.1-32.0	38.2	30.4	1.0
<i>Microptetix tasmanensis</i>	14	14	121.0-128.0	119.0-130.5	125.4	125.5	30.3-32.0	29.8-32.8	31.4	31.4	0.8
<i>Cavernotetix buchaniensis</i>	16	18	111.0-121.5	87.0-101.0	116.4	95.3	27.8-30.4	23.9-26.8	29.1	25.3	0.8
<i>Cavernotetix wyandensis</i>	12	8	104.0-119.5	90.5-98.5	114.2	99.3	27.8-30.3	23.8-26.0	29.2	25.1	0.9
<i>Cavernotetix montanus</i> ..	16	12	108.0-117.0	95.0-105.0	112.5	99.3	24.8-29.3	23.8-26.3	28.0	24.9	0.9

TABLE 4

*Comparison of leg segment length in three species of Australian Rhabdophoridae*

Species	Leg Segment	Highest Mean	Equal Highest Mean
<i>Micropathus cavernicola</i>	Tarsus	17	6
<i>Pallidotettix nullarborensis</i>	Femur	19	4
<i>Pallidotettix nullarborensis</i>	Tibia	21	3

## FOOD PREFERENCES

Crop contents from specimens of *P. nullarborensis* collected from nine Nullarbor caves have been analysed. Both live and preserved specimens were examined from Murra-el-elevyn Cave (N47), and preserved specimens from all other caves. All specimens were well nourished, and the full alimentary canals in all but one specimen indicated a plentiful food supply. A wide variety of plant and animal food is available in the caves and around the entrances, but marked preferences were noted for animal tissues (Table 5).

TABLE 5

*Crop Content of P. nullarborensis from nine Nullarbor Caves*

Caves	Number of Specimens Examined	Crop Content			
		Vertebrate Faeces and Tissues	Arthropod Tissues	Fungus	Angiosperm Tissues
N47	6	0	5	1	0
N38	4	0	5	1	1
N2	4	2	5	1	0
N59	6	0	3	2	3
N60	5	3	1	3	1
N48*	2	0	5	0	0
N51	3	0	5	0	0
N56	2	1	4	1	0
N140	1	0	0	0	3

The abundance of each category was rated on an arbitrary scale from 0 (absent) to 5 (very abundant).

\* From island in lake.

1. *Arthropods*

These form the main source of food for *P. nullarborensis*. Live arthropods are preyed on, and those found dead due to natural causes may also be eaten. Cannibalism is known to occur. It was not possible to identify any arthropod tissues precisely because of the small size of the particles; but no scales or parts of wings were detected.

2. *Vertebrates*

(a) *Faeces*. In most caves the walls, floor and talus slope beneath the roosting sites of birds are covered with faecal material. Mounds of bat guano also occur in a number of caves. They may be more extensive, but are not as common as bird guano. Of the 19 caves listed in Table 6. *P. nullarborensis* has been collected from 12, and in seven of these it was associated with bats. In a few caves it has been found on bat guano. Although guanobia may be commonly eaten, few traces of faecal material have been found in the crops of these rhabdophorids (Table 5).

(b) *Carcases*. Some caves act as animal traps, and carcasses of vertebrates form another food source for *P. nullarborensis* (Table 6). The remains of small animals brought into caves by dingoes, foxes and other predators may also be eaten.

TABLE 6  
Occurrence of vertebrate carcasses in 19 Nullarbor Caves

Caves	Bat	Dingo	Fox	Wombat	Rabbit	Cat	Rat	Bird	Snake	Lizard
N1	+	—	—	—	—	—	—	+	—	—
*N2	+	+	—	—	—	—	—	—	—	—
N3	+	+	—	—	—	—	+	+	+	—
*N4	+	—	—	—	—	—	—	+	+	—
*N7	—	—	+	+	+	—	—	—	—	—
N37	+	—	—	—	—	—	—	—	+	—
*N38	+	—	—	—	—	—	—	—	—	—
N45	—	—	—	—	—	—	—	+	—	—
*N47	+	—	—	—	+	—	—	—	—	—
*N48	+	—	—	—	+	—	—	+	—	—
*N49	+	—	—	—	—	—	—	—	—	—
*N51	—	—	—	—	—	—	—	—	—	+
*N53	+	—	—	—	—	—	—	—	—	—
*N59	—	—	—	—	+	+	—	—	—	—
*N60	—	—	—	—	+	—	—	+	—	+
N62	+	—	—	—	—	—	—	—	+	—
N63	+	+	—	+	+	—	+	+	+	+
N70	—	+	—	—	—	—	—	—	—	—
*N83	—	+	—	—	—	—	—	+	—	—

\* *P. nullarborensis* also occur in the cave.

(c) *Living Prey*. *P. nullarborensis* will also prey on small live vertebrates. In October 1966, they were observed to kill four unprotected kestrel chicks, *Falco cenchroides* Vigors and Horsfield, in a nest in the entrance shaft of Lynch Cave (N60). The rhabdiphorids attacked the backs of the chicks, and for two successive nights swarmed over and fed on the carcasses (Lowry, pers. comm.).

### 3. Plants

(a) *Fungi*. In the high humidity of the Nullarbor caves fungi grow readily on faeces and rotting wood. They are commonly eaten by *P. nullarborensis*, although usually not in large quantities.

(b) *Algae and Bryophytes*. Near cave entrances blue-green algae have become established on the walls, and lichens and bryophytes may also occur. No traces of these plants have been found in the crop of *P. nullarborensis*.

(c) *Angiosperms*. Large quantities of decaying vegetation, consisting of branches, twigs and leaf litter, have been washed into most caves, but angiosperm tissues are not commonly eaten. Traces of them were found in the crop of one rhabdiphorid from Walpet Cave (N38) and one from Lynch Cave (N60), and large quantities in the crop of one rhabdiphorid from Horseshoe Cave (N59). Part of an anther and masses of pollen belonging to a species of *Chenopodiaceae* were the only contents in the crop of a rhabdiphorid collected near the entrance to Unnamed Cave (N140).

### ACTIVITY RHYTHMS

During the day *P. nullarborensis* are immobile in domes, alcoves or on walls of caves, but at night they move about over the walls and floors. In October 1966, on two consecutive nights between 18.00 hours and 5.00 hours,



Lowry (pers. comm.) made a series of observations on activity levels in Lynch Cave (N60). Sunset was timed at 18.29 hours Central Standard Time, and sunrise at 5.41 hours. On both nights the insects became active between 19.00 hours and midnight. On the first night activity was again observed at 4.15 hours, and had ceased by 5.00 hours. On the second night no activity was observed after midnight. Temperature and relative humidity were measured with a whirling hygrometer: During the whole period of activity the mean temperature in the main chamber was 55.5°F. (range 53°–58°F.) and the mean relative humidity 79% (range 75–84%), while outside the cave the mean temperature was 53.5°F. (range 42°–62°F.) and the mean relative humidity 63% (range 35–87%) (Lowry, 1967). Although observed in the entrance shaft, none of the insects emerged from the cave.

In February 1968, temperature and relative humidity readings were taken in three caves using a thermohygrograph and an Assmann psychrometer. The general behaviour of the rhabdiphorids in these caves agrees very closely with Lowry's 1966 records.

In Murrawijinie No. 1 Cave (N7), where a large collapse doline encroaches on it, the greater part of the cave is exposed to light. Here *P. nullarborensis* disappear into cracks in the limestone during daylight, and emerge onto the cave walls at dusk. In February emergence was timed at 19.30 hours Central Standard Time. Between 50 and 60 insects were observed on the walls until midnight. During this period the temperature ranged between 66° and 68°F., and the relative humidity from 80 to 86%.

At Murra-el-elevyn Cave (N47) between 21.30 and 22.30 hours, 12 *P. nullarborensis* were observed in the large doline outside the cave. Some had climbed about 200 feet up the steep talus slope almost to the surface. The night was calm and rain was falling. The cave temperature was 62° to 66°F., gradually rising further from the entrance, and the relative humidity ranged between 84 and 88%. The temperature in the doline was 62°F. and the relative humidity 98%. While little difference was noted between doline and cave temperature, in the doline there was a rise of 10% in relative humidity. Most rhabdiphorids appeared to have emerged from the cave, and the few inside were all close to the entrance.

At Lynch Cave (N60) four *P. nullarborensis* were observed at 4.00 hours moving about on the surface a short distance from the cave entrance. The night was fine, calm and dark, the temperature 60.5°F. and the relative humidity 94%. Other rhabdiphorids were observed in the entrance shaft of the cave. During the following day they remained inactive on the cave walls, and although they became active at night, and a few were seen in the entrance shaft about midnight, they did not emerge onto the surface. The second night epigeal climatic conditions were less favourable for them. The surface temperature was 70°F. at midnight, and fell to a minimum of 67°F. at 6.00 hours. The relative humidity reached a maximum of 78% at midnight, and between then and 6.00 hours fluctuated between 71 and 78%. At the same time the cave temperature was constant at 68°F. and the relative humidity ranged between 93 and 95%. The difference between cave and surface temperature is not significant, so the drop of about 20% in humidity was probably an important factor in inhibiting the activity of the rhabdiphorids. A similar drop in humidity in October 1966 could have prevented the insects from leaving the cave. This suggests that when a humidity gradient is set up at night between the cave and the surface, the rhabdiphorids move to or stay in the region of higher humidity.

## DISCUSSION

*Pallidotettix nullarborensis* is the third Australian species of Macropathinae for which the number of instars has been determined. Unlike some New Zealand species (Richards, 1961), sexual dimorphism in the number of instars is absent in all three Australian species, and both sexes pass through seven instars (Richards, 1968a). Comparison of the results in Table 1 with those obtained for *Micropathus cavernicola* and *M. tasmaniensis* shows that the fit of observed and calculated measurements for *P. nullarborensis* is not quite as good as that obtained for the other two species. The figures used in Table 1 are based on insects collected at various times of the year, whereas the Tasmanian specimens were all collected on the same day. Thus the results obtained for *P. nullarborensis* may partly be governed by variations in environmental conditions.

In all other Macropathinae examined by the author, the female develops several mature eggs at any one time, although only one egg is laid at each insertion of the ovipositor into the substratum. The egg of *P. nullarborensis* is larger than those in species of *Micropathus* Richards, *Cavernotettix* Richards and *Pallidoplectron* Richards and this may partly explain the reduction in number of eggs present.

The seasonal cycle of *P. nullarborensis* is quite different from that in *Micropathus cavernicola* and *M. tasmaniensis*. Although the numbers of specimens of *P. nullarborensis* collected at certain times of the year are small, a comparison with New Zealand species of Macropathinae (Richards, 1961) shows that while there is a difference of six months in the appearance of the various nymphal stages, the complete life cycle is of comparable length. The period of embryonic development is about seven months in *Gymnoplectron waitomoensis* (Richards), and about eight months in *Pallidoplectron turneri* Richards, as compared with a period of 11 to 12 months in *P. nullarborensis*. The duration of nymphal instars in *G. edwardsii* (Scudder), then known as *Pachyrhamma fascifer* (Walker), and *G. waitomoensis* is 15 to 16 months, as compared with about 11 to 12 months in *P. nullarborensis*, but there is a nymphal diapause between April and October in the New Zealand species, females remaining in sixth instar and males in seventh instar. The length of the adult instar ranges from six to nine months in *G. waitomoensis* and is about seven months in *G. edwardsii*, as compared with possibly five to six months in *P. nullarborensis*. Thus *P. nullarborensis* spends a longer period in the embryonic stage, and a shorter period in the nymphal instars. This may be explained by the possibility of the embryo undergoing a summer diapause, and the absence of a winter diapause during nymphal instars of this species. It is possible that climatic conditions in the Nullarbor caves (Richards, in press) may have influenced the seasonal cycle of *P. nullarborensis* as temperatures throughout the year are up to 10°F. higher than those recorded from New Zealand caves (Richards, 1956). While two generations are nearly always present in populations of *G. edwardsii* and *G. waitomoensis*, usually only one generation is represented in populations of *P. nullarborensis*.

The food available to *P. nullarborensis* is similar to that eaten by raphidophorids in other parts of the world (Chopard, 1938, 1959; Gangwere, 1961; Remy, 1931; Richards, 1962, 1968a). Raphidophorids are usually omnivorous scavengers, and Gangwere (1961) claims the variety of their diet is second to none except cockroaches and possibly field crickets. Table 5 suggests that *P. nullarborensis* is primarily carnivorous and does not normally go outside cave entrances at night to feed on surrounding vegetation. The absence of algae and bryophytes, and the almost complete absence of higher

plant tissues from its diet may be due to the unsuitability of the species of plants growing on the Plain and in the dolines (Richards, in press), unfavourable climatic conditions outside the caves, a plentiful food supply in the caves, or a preference for animal tissues. The latter is considered the most likely, as in Waitomo Cave, New Zealand, raphidophorids fed on decaying vegetation and grasses swept into the cave during floods and left stranded on the walls or floating on the surface of the underground stream (Richards, 1962).

As with other Macropathinae (Richards, 1962, 1968a), no lepidopterous remains have been found in the crop content. This is surprising, as *Monopis* sp. is associated with bird guano in some Nullarbor caves, *Agrotis infusa* Boisd. may sometimes occur inside caves, and the remains of *Dasytopodia selenophora* Guenée are dropped in caves by bats. In Europe, Trichoptera and Lepidoptera are the main arthropods eaten by raphidophorids (Remy, 1931).

Although the normal animal portion of the diet of raphidophorids consists of arthropods, they will also feed on carcasses of bats and birds (Chopard, 1959). Predation on vertebrates has been recorded for only two species, *P. nullarborensis* and *Rhaphidophora oophaga* Chopard (Chopard, 1959), and in both cases unprotected, newly hatched birds have been attacked.

More information is needed on the activity rhythms of *P. nullarborensis*. As with other Australian raphidophorids (Richards, 1965), rapidly changing light intensity at dusk and dawn has initiated the development of a bimodal activity rhythm. This consists of a period of activity commencing shortly after sunset, a quiescent period during the night, a renewed period of activity shortly before dawn, and a further quiescent period during daylight. However, the period of activity after sunset lasts for about five hours instead of three. Temperatures are similar to other records taken during periods of activity, but relative humidity may be up to 15% lower. Fluctuations in humidity influence the behaviour of *P. nullarborensis*, and they have not been observed in the epigeal region unless the humidity was over 90%. Rain does not inhibit their activities, and the rise in humidity together with the absence of moonlight cause them to emerge from the cave.

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## APPENDIX 1.

Caves referred to by their index number in Tables 5 and 6 are as listed below. A map showing their location may be found in Richards (in press).

- N 1 Warbla Cave  
 N 2 Weebubbie Cave  
 N 3 Abrakurrie Cave  
 N 4 Koonalda Cave  
 N 7 Murrawijinie No. 1 Cave  
 N37 Mullamullang Cave  
 N38 Walpet Cave  
 N45 Winbirra Cave  
 N47 Murra-el-elevyn Cave  
 N48 Cocklebiddy Cave  
 N49 Pannikin Plain Cave  
 N51 Gecko Cave  
 N53 Moonera Tank Cave  
 N56 Tommy Grahams Cave  
 N59 Horseshoe Cave  
 N60 Lynch Cave  
 N63 Thylacine Hole  
 N70 Firestick Cave  
 N83 Old Homestead Cave  
 N140 Unnamed Cave